

## Original Articles

## A generic method to assess species exploratory potential under climate change



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## ABSTRACT

Climate, by altering the spatio-temporal distributions of suitable habitats, leads to modifications in a multitude of species ranges. In recent years, the ability of species to adjust to changing climatic conditions is of growing concern. In the present study, a generic trait-based method to assess species exploratory potential under climate change is proposed. “Exploratory potential” is here defined as the capacity of species to initiate the act of leaving their current habitats and to reach new ones outside of their range, at a rate fast enough to keep pace with climate change. The presented method is based on the calculation of the Exploratory Potential Index (EPI), a metric that combines several life-history traits into a single numeric value. Both coefficients and variables of this composite metric are flexible. They depend on the set of species under consideration through a two-step participatory expert-based procedure. A panel of experts on the species’ biology, ecology and conservation is first to be constituted. Then, experts are separately consulted to validate the variables to be integrated in the composite EPI index and are asked to rank the importance of these variables relative to each other following an Analytic Hierarchy Process. Coefficients in the EPI index and scores are given a credibility distribution using a Bayesian inference model. Anadromous species are chosen as a first application case. Scripts and raw survey data are made available to readers to ease applications to other species groups.

## 1. Introduction

Evidence that species are shifting their latitudinal distributions, elevation ranges, phenologies (Parmesan, 2006; Poloczanska et al.,

2013), and body sizes (Daufresne et al., 2009; Gardner et al., 2011) in response to recent climate change is accumulating rapidly. However, given the rapid rate at which climate is changing, the ability to move in response to environmental change does not necessarily mean that all

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taxa will track those changes appropriately to survive (e.g. Bertrand et al., 2011; Comte and Grenouillet, 2013).

The exploration of the environment by individuals through any movement phenomena is a central process for biodiversity to adapt to environmental variability and change (Jeltsch et al., 2013), but remains generally poorly known due to methodological and technological challenges related to tagging and tracking, creating data-poor situations (i.e. few quantitative estimates of dispersal (Bradbury et al., 2008)) and often leads to strong assumptions in range shift modeling (e.g. Bateman et al., 2013; Hellmann et al., 2016). As such, bringing valuable and substantial insight on the exploration of new and alternative territories by a large set of species at a time is a core challenge in the anticipation of biodiversity distributional response to climate change (Travis et al., 2013). This challenging task could be envisaged through trait-based approaches. Indeed, various studies have demonstrated that species' traits can be good predictors of response to climate change with methods relatively rapid to implement (Angert et al., 2011; Chessman, 2013; Jiguet et al., 2007; Pearson et al., 2014; Perry et al., 2005; Sunday et al., 2015). However, linking the exploratory potential to biological traits for a given set of species requires conceptual and methodological developments that are addressed in the present paper. We make this effort more tractable by working initially on: (i) species that travel long distances to complete their life cycle, are characterized by populations with multiple migratory strategies and thus are more likely to respond to climate change by modifying their distribution range within a rather short time frame; and (ii) species for which comprehensive information on species traits can be easily found in open-access biodiversity databases.

Anadromous fishes, i.e. species that reproduce in continental watersheds and mature in marine waters (McDowall, 1988), appear particularly suitable to formalize the influence of traits in predicting the ability of species to move towards the poles in response to climate change. During past glaciations, they retracted to southern refugia and then, as the ice sheets retreated, reinvaded the river systems (McDowall, 1988). The contemporary success of anadromous species in reaching a new location and establishing a population has been recently demonstrated with various examples (e.g. Hasselman et al., 2012; Labonne et al., 2013). In addition, their breeding migration is often characterized by high site fidelity, with most adults returning to the river of their birth (i.e. natal homing) and a few individuals straying to other spawning areas (Cury, 1994; McDowall, 2001). In some cases, this homing rate has been precisely estimated (Walther et al., 2008) and appears variable among species, an interesting feature when investigating links that exist between life history traits and distribution changes. More broadly, anadromy and homing/straying are two behavioral life-history traits for which our understanding benefits from decades of worldwide studies (Keefer and Caudill, 2014; Roule, 1914). Moreover, multi-species trait-based approaches have unequivocally identified diadromous fish as high conservation concern (Branco et al., 2008) and high vulnerability to climate change (Hare et al., 2016). But beyond that, focusing on diadromous fish is relevant given their low number of representatives (Eschmeyer and Fong, 2016), their poor conservation status (Limburg and Waldman, 2009) and their enormous economic value (e.g. Amin et al., 2004; Kobayashi et al., 2015).

The aim of this method paper is to develop a generic, trait-based metric to score species by their exploratory potential. To increase reliability, the proposed metric combined several ecologically meaningful variables (life-history traits hereafter) into an overall species score to represent the consensus emerging from specialists. To increase applicability, the proposed metric had to be adjustable to be used on a wide range of taxa following a standardized and fully detailed protocol. A first numerical application of the method and the metric was made on North Atlantic Ocean anadromous fishes, identified as relevant biological models.

## 2. Material and methods

The exploratory potential index (EPI) that we developed in the present work relied on a conceptual framework and an expert-based participatory procedure adapted from analytical hierarchy process (AHP) theory (Saaty, 1987; Saaty, 2008). The approach can be summarized in four main phases: (i) problem modeling/conceptualization (Section 2.2); (ii) elicitation of experts' opinions (Section 2.3); (iii) 'translation' of these expert opinions into weights (Section 2.4); and (iv) calculation of the final EPI index for each species of interest, based on weights, and data on life-history traits (Section 2.5).

### 2.1. Exploratory potential definition and limits

Within the diversity of range shift patterns that were described in the scientific literature, half of them involved expanding leading edges (Maggini et al., 2011), driving species towards the poles (Parmesan, 2006). As such, we focused on species life-history traits that enhance the intrinsic capacity of populations to send individuals outside of the current species distribution range. The selection of life-history traits is thus confined to the departure and transfers during the dispersal process (Clobert et al., 2012), as the subsequent establishment phase is characterized by extrinsic parameters such as habitat connectivity and suitability. Complex mechanisms such as adaptive evolution and phenotypic plasticity, by which species can track changing environments and also increase their exploratory potential, are not considered at this stage (Fig. 1).

### 2.2. The 'problem' modeling/conceptualization phase

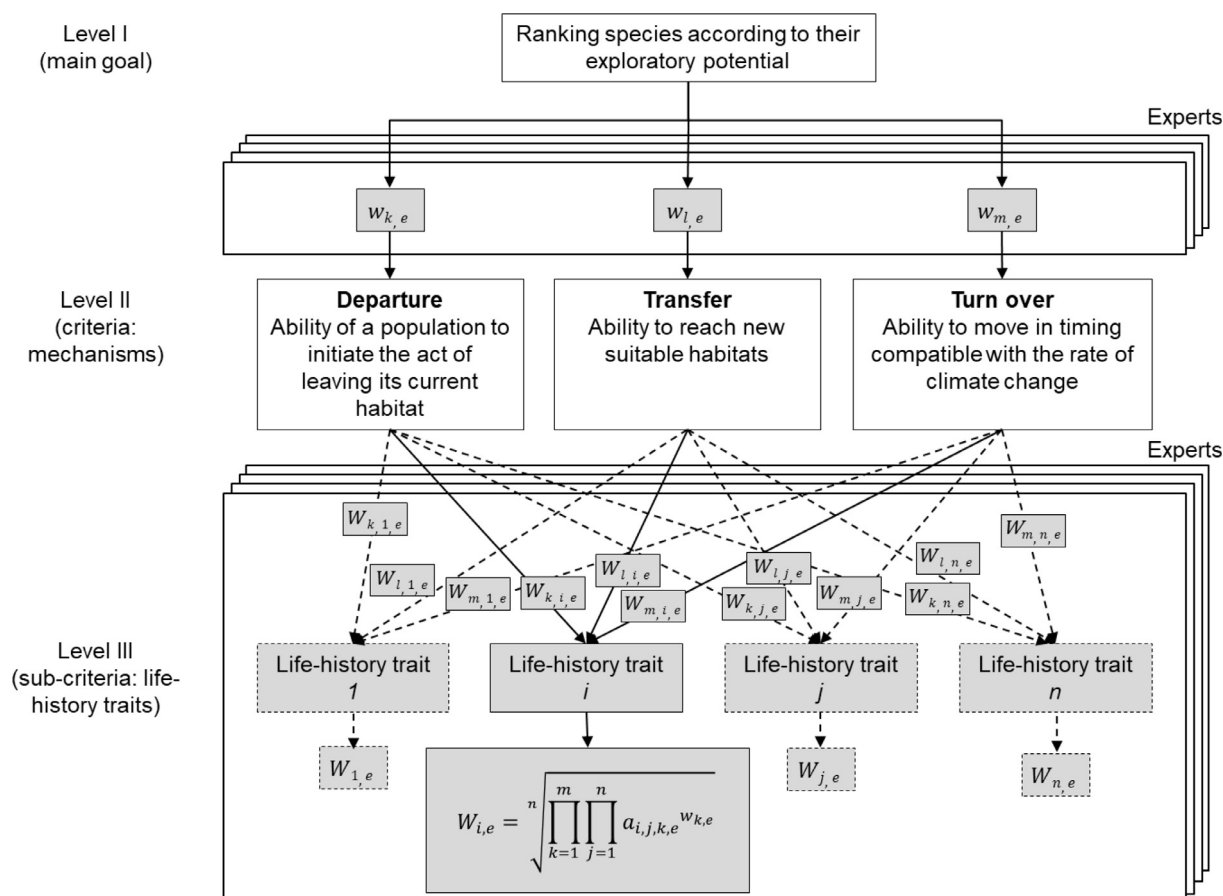
The originality of the AHP method consists in decomposing a complex issue into a hierarchy of more easily comprehensible sub-problems, with the possibility to analyze them independently. The present 'problem' was structured into three fixed levels (Fig. 1). Level I is the goal itself that is comparing the exploratory potential of different species. Level II corresponds to the decomposition of the core problem into ecological mechanisms applicable to a large range of taxa. Three mechanisms (i.e. level II in Fig. 1) were predefined by the project leaders (i.e. persons who initiated the process for a given species group) based on major syntheses on dispersal and climate change biology (e.g. Clobert et al., 2012; Lenoir and Svenning, 2013; Pearson, 2006): (i) the ability for populations at the leading edge to initiate the act of leaving their current habitats (departure); (ii) the ability to 'physically' reach new suitable habitats (transfer), and (iii) the ability to match this range shifting response with climate change velocity (turnover rate). Level III is constituted of life-history traits which depend in numbers and nature upon case studies (i.e. the species group under interest) and data availability (Fig. 1).

### 2.3. Eliciting experts' opinions

Formal elicitation methods have increasingly been developed and applied to incorporating expert knowledge in ecology (Fletcher, 2005; Kuhnert et al., 2010; Martin et al., 2012; McBride et al., 2012; Roy et al., 2014; Uusitalo et al., 2005).

A preliminary list of species and a geographic area should be set by project leaders. In accordance with these elements, a panel of experts must be then constituted. The questions that experts will be asked to answer will reflect, to some point, their in-depth knowledge of the species biology and ecology, and their understanding of climate change impacts (Fazey et al., 2006). As such, one of the main criteria for panel constitution is that experts come from various institutions and countries covering, among other things, a large part of the investigated species ranges.

The interview was structured into four successive tasks (see form in Appendix A). The first task was to learn about the definition and limits



**Fig. 1.** EPI hierarchical design. White boxes are fixed elements of the method that should remain the same when the method is applied to other species groups (i.e. main scope, mechanisms and the decomposition into three levels). On the contrary, gray boxes corresponded to method features that could be adapted to the species group (i.e. life-history traits) or weight numerical values that vary depending on the application case.

**Table 1**

Modalities for the five life-history traits retained in the EPI index. Modalities were ordered by increasing favorability in terms of exploration potential.

	Modality 1	Modality 2	Modality 3	Modality 4
Age at first maturity (year) <i>Age<sub>mat</sub></i>	First reproduction at an age greater than 6	First reproduction at the age of 3–6	First reproduction at the age of 2–3	First reproduction at the age of 1
Body size at first maturity (cm) <i>L<sub>mat</sub></i>	$L_{mat} \leq 30$	$30 < L_{mat} \leq 90$	$90 < L_{mat} \leq 200$	$200 < L_{mat}$
Distance between spawning and feeding habitats <i>Dist</i>	Estuarine species	Marine phase is shared between estuaries and short-range coastal migrations	Marine phase is characterized by coastal migrations up to 1000 km	Marine phase is characterized by large scale migrations (> 1000 km)
Homing rate <i>Hom</i>	Strong homing ( $\geq 90\%$ )	Homing	No homing detected or uncertain	Panmixia
Number of reproduction events <i>N<sub>repro</sub></i>	Semelparous	Individuals reproducing no more than twice during their life and with discontinuous reproduction events among years	Species with individuals reproducing every year	Species with individuals reproducing every year and continuously during long periods of time

of exploratory potential, and its structural framework of three critical mechanisms (levels I and II in Fig. 1). The second task was to approve or modify a pre-defined species list established by project leaders. The third task was to validate a pre-defined list of life-history traits (i.e. Level III in Fig. 1) that vary predictably, to some extent, with exploratory potential and that may apply best to at least one of the three mechanisms (i.e. Level II in Fig. 1). These validated life-history traits are the variables in the EPI index. A critical point also considered during their selection by project leaders was the fact that values should be obtained for most species and populations in their natural environments. Finally, the last task was to assign weights reflecting the relative importance between the mechanisms and between the validated life-

history traits within each mechanism. Outputs from this task are the coefficients/weights in the EPI index. Weights are kept the same for an entire group of species, and life-history traits values vary according to the species of interest (Table 1).

## 2.4. Estimating weights in the composite EPI index

### 2.4.1. General principles

In the AHP method, expert opinions are expressed through pairwise comparisons of criteria or sub-criteria in matrices according to a proposed judgment scale with verbal gradations and associated numerical values. Here, we retained the geometric judgment scale of Lootsma

(1993) (see form in Appendix A). Each expert's opinion is recorded in a  $n \times n$  matrix ( $A$ ):

$$A = \begin{bmatrix} 1 & a_{12} & \cdots & a_{1n} \\ a_{21} & \cdots & a_{ij} & \cdots \\ \cdots & a_{ji} = 1/a_{ij} & \cdots & \cdots \\ a_{n1} & \cdots & \cdots & 1 \end{bmatrix} \quad (1)$$

where  $a_{ji}$  is the comparison between elements  $j$  and  $i$ ,  $n$  is the number of evaluation criteria considered (e.g. here,  $n = 3$  at Level II and  $n = 5$  at Level III; Fig. 1). Each entry  $a_{ij}$  of the matrix  $A$  represents the importance of the  $i$ th criterion (row) relative to the  $j$ th criterion (column). If  $a_{ij} > 1$ , then the  $i$ th criterion is more important than the  $j$ th criterion, while if  $a_{ij} < 1$ , then the converse is true. If two criteria have the same importance, then the entry  $a_{ij}$  is 1. The entries  $a_{ij}$  and  $a_{ji}$  also satisfy the following transitivity constraint:

$$a_{ij} \times a_{ji} = 1 \quad (2)$$

Once the matrix  $A$  is filled in, the criteria weight vector  $w$ , which is an  $n$ -dimensional column vector, is derived by calculating the geometric mean for each row of the matrix.

Assuming a single expert  $e$  filling matrix  $A$ , the weight of criterion  $i$  ( $w_{i,e}$ ) can be derived as follows:

$$w_{i,e} = \sqrt[m]{\prod_{j=1}^m a_{ij,e}} \quad (3)$$

where  $a_{ij,e}$  is the comparison of criterion  $i$  relative to criterion  $j$  by expert  $e$  and  $m$  the number of criteria in matrix  $A$ . Then, 'impact' scores can be obtained by normalizing  $w_{i,e}$  (i.e. dividing by the sum of all criterion weights) making sure the scores add up to 1.

As weights make sense only if derived from consistent or near consistent matrices, a consistency check must be applied to pairwise comparisons produced by every expert. Crawford and Williams (1985) suggested using the sum of the differences between the ratio of the calculated weights and the given comparison in the Geometric Consistency Index (GCI) for all pairs of criteria in matrix  $A$ :

$$GCI = \frac{2}{(n-1)(n-2)} \sum_{i < j} \left( \log a_{ij} - \log \frac{w_i}{w_j} \right)^2 \quad (4)$$

A perfectly consistent expert should always obtain  $GCI = 0$ . Small values of inconsistency may be tolerated by using the criteria proposed by Aguaron and Moreno-Jiménez (2003), i.e. a GCI value of 0.3147 for  $n = 3$ , a GCI value of 0.3526 for  $n = 4$  and a GCI value of 0.370 for  $n > 4$ ;  $n$  being the criteria in matrix  $A$ . When the GCI value is greater than the previous thresholds, the most inconsistent judgment, i.e. the larger difference in Eq. (4), could be revised in the sense of approximating  $a_{i,j}$  to  $w_i/w_j$ .

#### 2.4.2. Weight aggregation: A multiple-level AHP

When decomposing a 'problem' into a hierarchical structure following the AHP method, within each level of the hierarchy, the relative importance between each pair of criteria (or among pairs of sub-criteria to an upper single criteria) is evaluated. In the present application case, four pairwise comparison matrices  $A$  have to be filled by each expert: (i) a weight to each mechanism was assigned applying Eq. (3) on the matrix  $A$  at Level II; and (ii) a weight to each trait with respect to a given mechanism (i.e. local weights) was calculated using Eq. (3), and the corresponding matrix  $A$  at Level III.

The next step is thus to synthesize the local weights of traits across all mechanisms (i.e. Level II in Fig. 1) to determine the global weight of these traits (i.e. level III in Fig. 1). Assuming a single expert  $e$ , the global trait weights ( $W_{i,e}$ ) of trait  $i$  by expert  $e$  were determined as the geometric mean across all three mechanisms:

$$W_{i,e} = \sqrt[n]{\prod_{k=1}^m \prod_{j=1}^n a_{i,j,k,e}^{w_{k,e}}} \quad (5)$$

where  $a_{i,j,k,e}$  is the comparison between trait  $i$  and  $j$  according to mechanism  $k$  by expert  $e$ ,  $w_{k,e}$  the weight of mechanism  $k$  at Level II by expert  $e$ ,  $m$  the number of mechanisms at Level II, and  $n$  the number of traits at Level III. Impact scores can be obtained by normalization of  $W_{i,e}$  making sure the scores add up to 1 for each expert.

#### 2.4.3. Identification of potential experts groups

We performed a hierarchical clustering analysis (HCA) on mechanism weights  $w_k$  to highlight whether we had a consensus among experts regarding the broad mechanisms behind the species exploratory potential or, on the contrary, groups supported by different ecological paradigms. The identification of these potential divergences is important as it could lead to different rankings of species and thus conservation recommendations. Clustering not explained by ecological theories should not be retained as meaningful. For HCA, we used the Ward's linkage method and Euclidean distances. To determine the optimal number of clusters, a plot of linkage distance as a function of number of clusters was examined, looking for the point of maximum curvature.

#### 2.4.4. Aggregation of multiple expert opinions

To estimate the overall trait weights  $W_i$ , we assumed that experts weights followed a Dirichlet distribution:

$$(W_{1,e}, \dots, W_{n,e}) \sim \text{Dirichlet}(W_1, \dots, W_n) \quad (6)$$

This formulation accords the same importance to each expert of the panel and accounts for their variety with a distribution probability.

We assigned a normal diffuse prior to each  $W_i$  with the sum of probabilities equal to unity. Then,  $W_{i,e}$  were used to update the prior distributions. The Bayesian inference model was implemented using the software JAGS (Plummer, 2003) and was run using package 'rjags' (Denwood, 2016) in R 3.2.5 (R Core Team, 2016). Three independent parallel chains were run for 50 000 iterations after a burn-in period of 10 000 iterations. Convergence diagnostics were made using the 'coda' library (Plummer et al., 2006). Tests of Gelman and Rubin (1992) and visual inspection of a posteriori distribution were carried out for validation.

#### 2.5. EPI index calculation

##### 2.5.1. Coding life-history traits

The amount and precision of available data among the species of interest could be highly variable. Adding to this, a mix of quantitative and qualitative life-history traits could be the best final selection for a given group of interest. As such, data on life-history traits should be preferentially coded. We recommend using a number of modalities constant across variables (Table 1). Nevertheless, for each variable, 1 has to be associated to the supposedly least favorable characteristic and 4 with the most in terms of exploration potential (see section 2.6.2 for justifications regarding variable favorability trends). Cutpoints for quantitative variables such as age or size should be defined with the goal of providing contrasting ecological meaning to categories.

##### 2.5.2. EPI calculation

For a given species  $s$ ,  $EPI_s$  is calculated as the sum of the products of overall trait weights combined with standardized data of each biological trait:

$$EPI_s = \sum_{i=1}^n W_i \times P_{i,s} \quad (7)$$

where  $W_i$  is the overall weight for trait  $i$ ,  $n$  is the number of traits,  $P_{i,s}$  is the normalized value of the data of trait  $i$  for species  $s$ , corresponding to



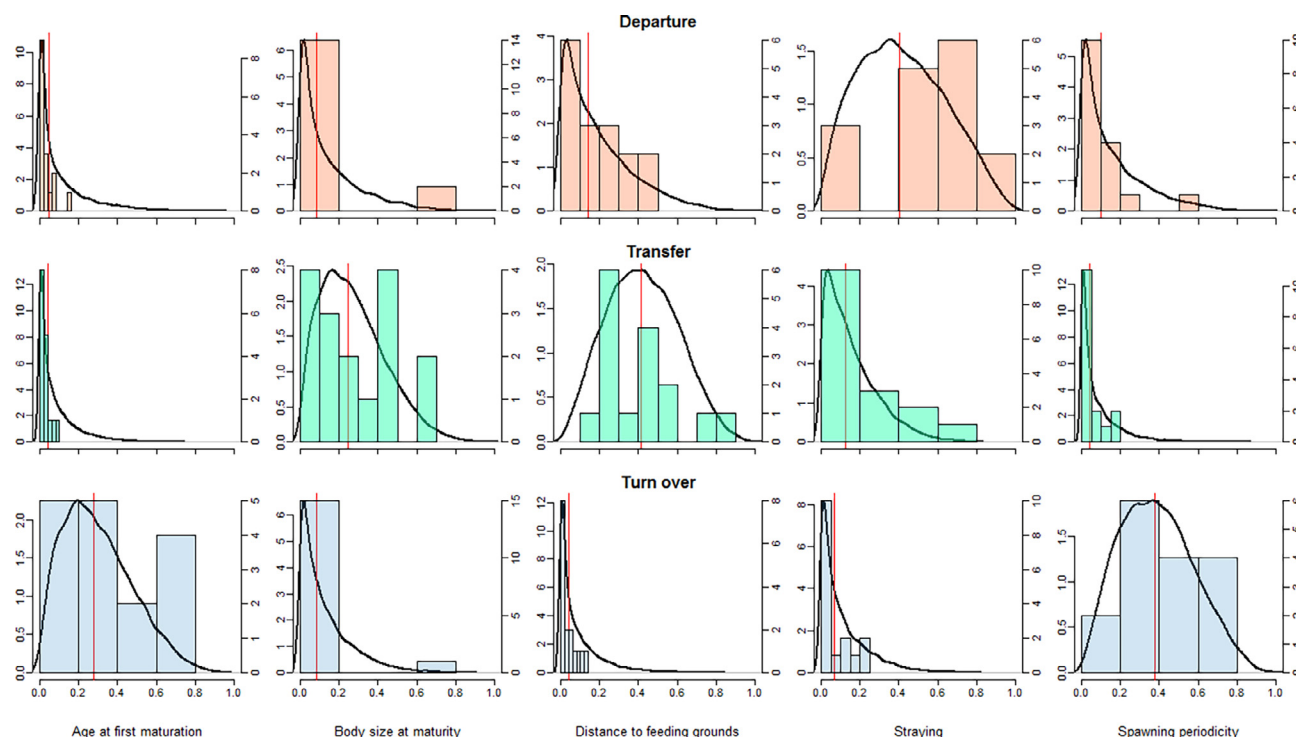


Fig. 2. Relative weights for the 5 selected life-history traits according to the 3 mechanisms. Density plots represent the estimated distribution (first y-axis) and colored bars the expert opinions (second y-axis). The red line is the distribution median (see Table 4 for values and standard deviations).

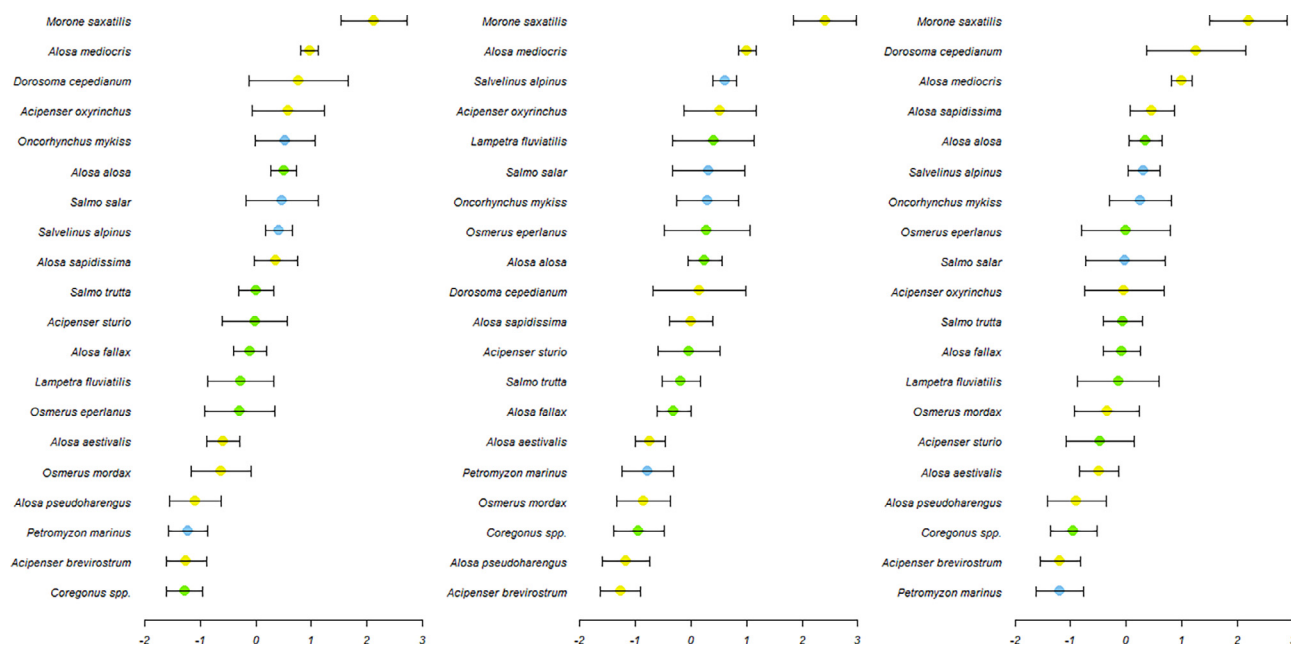


Fig. 3. EPI distribution values for the anadromous fish of the northern Atlantic Ocean according to the three groups of experts. Means are given with their standard deviation. North American species are in yellow, European ones are in green and blue represents species occurring on both sides of the Atlantic Ocean as listed in Table 2. Classifications are given in the order of groups in Table 3.

the modality of trait  $i$  for species  $s$  divided by the maximum modality of trait  $i$ . Since  $W_i$  is associated to a posterior distribution (Section 2.4.4), this process results in a credibility distribution per species. The mean of the credibility distribution was used as the best EPI estimator in Fig. 3.

All the calculations described in Sections 2.4 and 2.5 were coded into R. Raw survey data and R scripts are provided in Appendix B and could be easily set for any group of species by providing file paths to pairwise comparison matrices and categorized ecological data stored into Excel files.

## 2.6. Application to North Atlantic anadromous fish

### 2.6.1. Anadromous species of the North Atlantic and species experts

We narrowed down the list of Limburg and Waldman (2009) to species only frequenting the North Atlantic coast and with numerous populations identified. Moreover, the list was modified as follows. Atlantic sturgeon (*Acipenser oxyrinchus*), native to the North American fauna and for which past occurrences in European waters have been recently registered, was considered as inhabiting both coasts (Chassaing

**Table 2**

List of North Atlantic anadromous fish considered in the present study with original reproductive range and current IUCN species conservation status (adapted from Limburg and Waldman, 2009). WA and EA corresponded to Western and Eastern Atlantic coast respectively. *Coregonus huntsmani* was not taken into account because of its extremely narrow original distribution range restricted to two populations in the US. *Oncorhynchus mykiss*\*, the Rainbow trout, was added to the analysis as an ubiquitous species. The species is not listed by the IUCN. An asterisk \* indicates species listed as ‘endangered’ in the U.S. Endangered Species Act of 1973.

Coast	Common name	Latin name	Reproductive range	Conservation status
WA	Sea lamprey	<i>Petromyzon marinus</i>	Florida to New Brunswick	Least concern
WA	Shortnose sturgeon*	<i>Acipenser brevirostrum</i>	Florida to New Brunswick	Vulnerable A2ce; B1ab(iii)
WA	Atlantic sturgeon*	<i>Acipenser oxyrinchus</i>	Mississippi to Quebec (+ past occurrences in Northern Europe)	Near Threatened
WA	Alewife	<i>Alosa pseudoharengus</i>	South Carolina to Newfoundland	Least concern
WA	Blueback herring	<i>Alosa aestivalis</i>	Florida to Nova Scotia	Vulnerable A2b
WA	Hickory shad	<i>Alosa mediocris</i>	Florida to Maine	Least concern
WA	American shad	<i>Alosa sapidissima</i>	Florida to Quebec	Least concern
WA	Gizzard shad	<i>Dorosoma cepedianum</i>	Texas to Maine	Least concern
WA	Arctic char	<i>Salvelinus alpinus</i>	Newfoundland to Arctic Ocean	Least concern
WA	Atlantic salmon*	<i>Salmo salar</i>	Connecticut to Quebec	Lower risk/Least concern
WA	Rainbow smelt	<i>Osmerus mordax</i>	Delaware to Labrador	Least concern
WA	Striped bass	<i>Morone saxatilis</i>	Louisiana to Quebec	Least concern
EA	Sea lamprey	<i>Petromyzon marinus</i>	The Western Mediterranean to Greenland/Norway	Least concern
EA	River lamprey	<i>Lampetra fluviatilis</i>	The Western Mediterranean to Finland	Least concern
EA	European sturgeon	<i>Acipenser sturio</i>	Black Sea to the Baltic Sea	Critically Endangered A2cde; B2ab(ii,iii,v)
EA	Allis shad	<i>Alosa alosa</i>	Morocco to Germany + UK	Least concern
EA	Twaite shad	<i>Alosa fallax</i>	Morocco to Lithuania	Least concern
EA	Nordic coregonids	<i>Coregonus</i> spp.	Netherlands to Russia	Not applicable
EA	Arctic char	<i>Salvelinus alpinus</i>	Sweden to the Arctic Ocean	Least concern
EA	Atlantic salmon	<i>Salmo salar</i>	Portugal to Greenland	Lower risk/Least concern
EA	Sea trout	<i>Salmo trutta</i>	Portugal to Russia	Least concern
EA	European smelt	<i>Osmerus eperlanus</i>	France to Russia	Least concern

et al., 2013). Whitefish is a group of populations, forms, or species with unclear taxonomy, and some presenting an anadromous behavior (Østbye et al., 2005). Given these uncertainties, data on anadromous whitefish were all recorded under the name *Coregonus* spp. Rainbow trout, *Oncorhynchus mykiss*, and Gizzard shad, *Dorosoma cepedianum*, were both added to the list. The first has been introduced worldwide while the second was only recently observed as anadromous (Table 2).

Experts were identified from: (i) the collaborative network of the project leaders specializing in diadromous fish conservation; (ii) the Diadfish network (www.diadfish.org); and (iii) researchers working on species invasions and climate change impacts.

### 2.6.2. Specific life-history traits

Five life-history traits were selected by project leaders as relevant in terms of exploratory potential: distance between spawning and feeding habitats (*Dist*), homing rate (*Hom*), body size at first maturity ( $L_{mat}$ ), number of reproduction events ( $N_{repro}$ ) and age at first maturity ( $Age_{mat}$ ) (Table 1).

Jiguet et al. (2007) failed to identify the migratory index, defined as the distance between breeding and wintering grounds, as a predictor of recent population changes in common breeding birds. Here, the distance between spawning and feeding habitats (*Dist*) is selected but in association with the other life-history traits presented below. Exploratory potential is assumed to increase with increasing distances between the spawning and feeding grounds.

Anadromous fishes are well known for their homing tendencies (McDowall, 1988). Estimates of river level homing average between 90 and 100% in many salmonids (Keefer and Caudill, 2014). In contrast, lampreys with a parasitic adult phase are strongly suggested not to express a precise homing behavior but rather to exhibit a regional panmixia (Waldman et al., 2008). In any case, straying can be viewed as an ‘exploratory behavior’ that can contribute to fish population persistence, colonization, and range expansion (Secor, 1999). Also, a strong natal homing enhances local adaptation by limiting gene flow between populations. As such, it can limit the ability to population to range shift effectively (Crozier et al., 2008). The exploratory potential should intuitively increase with decreasing homing rate (*Hom*).

Body size is a major factor shaping the propensity and ability of species to disperse (McCauley and Mabry, 2011; Sutherland et al., 2000) and has the advantage of being a datum readily available for a vast majority of species. Recently, life-history and morphological characteristics related to species dispersal ability appeared especially important to explain altitudinal colonization in resident stream fish assemblages (Comte et al., 2014). In Winemiller and Rose (1992), highly migratory fishes were associated with particular life-history strategies characterized, among other traits, by large body size. As such, the exploratory potential is strongly hypothesized to increase with body size at first maturity ( $L_{mat}$ ).

Iteroparity is now conventionally viewed as an adaptation to uncertain environments related to variations in juvenile survival (Wilbur and Rudolf, 2006). Interestingly, within anadromous populations, Limburg et al. (2003) compiled evidence of increasing percent of repeat spawners with latitude for shads. Moreover, for iteroparous species, dispersal is something that occurs throughout the lifetime or, at least, in multiple occasions. Exploratory potential is consequently assumed to increase with increasing number of reproduction events during a lifetime ( $N_{repro}$ ).

Perry et al. (2005) demonstrated that demersal fish with life-history traits associated with fast population growth responded more strongly to climate change. Among others, shifting species exhibited faster maturation or smaller age at first maturity ( $Age_{mat}$ ), confirming that this trait is linked to species resilience as primarily asserted by a panel of fisheries scientists of the American Fishery Society (Musick, 1999).

For the five life history traits, project leaders defined four modalities (Table 1; see Section 2.5.1) and classified each species in one of these modalities using data from the literature (see Appendix C). Traits and their modalities were finally submitted to the judgement of experts.

## 3. Results

Sixteen scientists agreed to participate and were then elicited through a single iteration questionnaire (see the form in Appendix A) via videoconference or face-to-face interviews. The hierarchical structure of the analysis was not much questioned, nor were the predefined

**Table 3**

Global mechanism weights,  $w_i$  (i.e. median and standard deviation according to the Bayesian inference model) attributed by the 16 experts to the 3 mechanisms. Groups referred to the HCA performed on these values. Code for expert names is given in Table A.1 in Appendix A.

		Group 1	Group 2	Group 3
Departure	Median	0.12	0.60	0.39
	SD	0.11	0.11	0.14
Transfer	Median	0.44	0.27	0.09
	SD	0.16	0.10	0.10
Turn-over	Median	0.39	0.11	0.49
	SD	0.16	0.08	0.15
Number of experts		7	6	3
Expert code		3, 7, 8, 9, 10, 13, 16	2, 4, 5, 11, 14, 15	1, 6, 12

life-history traits. However, the species list in Table 2 was debated and modified accordingly, as stated in Section 2.6.1.

Spearman rank correlation tests performed on categorical life-history traits did not reveal high correlations and thus information redundancy (i.e. all  $r_s < 0.4$ ) (Table 1). When checking the Bayesian inference model, the low value of the Gelman-Rubin diagnostic (i.e. close to 1 for every node of the model) ensures the convergence of the Markov Chain Monte Carlo chains.

Regarding the relative importance of each mechanism in the exploration process (i.e. first pairwise comparison matrix used to calculate overall mechanism weights), all the matrices were consistent according to the GCI index. Three groups of experts emerged from the HCA (Table 3). The opinion shared by 44% (i.e. 7 of 16) of the experts was that the ability to transfer and the turnover rate of a species play equal roles in the exploratory potential (i.e. median  $\pm$  standard deviation:  $0.44 \pm 0.16$  and  $0.39 \pm 0.16$ , respectively; Table 3). Shared by 38% of the experts, another vision was that of a departure mechanism considered as the most important process (i.e.  $0.60 \pm 0.11$ ). The third emerging pattern (18% of the experts) was that the exploratory potential mainly depends upon both the turnover rate (i.e.  $0.49 \pm 0.15$ ) and the departure ability (i.e.  $0.39 \pm 0.14$ ).

Regarding the importance of life-history traits in driving a specific mechanism, matrices were generally inconsistent, reflecting most probably the difficulty for experts to compare more than three items (Level III in Fig. 1). Nonetheless, results are close to a consensus among experts (Table 4; Fig. 2). Across all experts, the ability to depart (i.e. first mechanism at Level II; Fig. 1) mainly depends upon the homing rate (i.e. median  $\pm$  standard deviation:  $0.45 \pm 0.21$ ), while the distance between spawning and feeding habitats, and the size at first maturity are preferred proxies (i.e.  $0.38 \pm 0.16$  and  $0.30 \pm 0.19$ , respectively) for the ability of a species to transfer. Regarding the

**Table 4**

Overall trait weights,  $W_i$  (i.e. median and standard deviation according to the Bayesian inference model) of the 5 selected life-history traits according to the 3 mechanisms.

		Departure	Transfer	Turn-over
Age at first maturity (year) $Age_{mat}$	Median	0.05	0.04	0.30
	SD	0.127	0.10	0.16
Body size at first maturity (cm) $L_{mat}$	Median	0.05	0.21	0.07
	SD	0.125	0.16	0.11
Distance between spawning and feeding habitats $Dist$	Median	0.14	0.38	0.035
	SD	0.16	0.19	0.11
Homing rate $Hom$	Median	0.45	0.16	0.04
	SD	0.21	0.15	0.09
Number of reproduction events $N_{repro}$	Median	0.10	0.04	0.43
	SD	0.14	0.11	0.17

turnover ability, experts' opinions indicate that the number of reproduction events and the onset of first maturity are the most important traits among the selected ones (i.e.  $0.43 \pm 0.17$  and  $0.30 \pm 0.16$ , respectively) (Table 4). Each trait was alternatively considered as the most important depending on the mechanism considered. These conclusions associated to the hierarchical structure of the problem led to mean coefficients in the EPI index close to 0.2 for each of the five traits, i.e. the simplest model with equal weights. The same was observed within each expert group variables (i.e. mean/standard deviation:  $0.18 \pm 0.04$ ,  $0.18 \pm 0.08$ ,  $0.18 \pm 0.04$  for group 1, 2 and 3, respectively). As such, species at the bottom of the ranking were those exhibiting systematic low (1 or 2) modalities for the five life history traits (Table 1).

Considering expert groups separately, all the species in the top ten remained the same across the three rankings (Fig. 3). The striped bass, *Morone saxatilis*, was the species with the highest EPI index. With regard to the probability distribution per species, EPI values for the striped bass did not encompass any other distribution in the first two groups. No marked geographical pattern was noticed: species from one side of the Atlantic were not exhibiting more or less exploratory potential. The three species, which are of most concern in the IUCN red list of endangered species were also in the lower half of the rankings, namely *Acipenser sturio*, *A. brevirostrum* and *Alosa aestivalis* (Table 2). They composed the bottom of the ranking with *Petromyzon marinus*, *Alosa pseudoharengus* and *Coregonus* spp.

#### 4. Discussion

From a methodological point-of-view, applying the EPI methodology to a group of species does not require extensive data collection, transformation and normalization, or computational time. As such, the EPI index can be used on a list of species with different levels of knowledge on their life history and, more broadly, with distinct economic and ecological values. Consequently, the EPI index could contribute to a multi-species conservation approach by the identification of species at risk, even among 'non-targeted' ones. In addition, future applications will benefit from the increased availability of large databases on life-history traits. However, establishing the list of species in future applications should be given particular attention. The list should be restricted to species comparable in terms of biogeography and life cycle at a minimum to secure the selection of meaningful life-history traits and to ease the work of experts when filling the pairwise comparisons matrices. Interestingly, different means of results' validation can be envisaged. EPI scores can be compared to empirical data such as the species historical distribution ranges. Species with a large range might infer more effective post-glacial recolonization. EPI scores can also be compared to simulated data from species-specific distribution models.

Beyond the application of the EPI methodology to other groups of species, our study represents a formal framework to elicit expert opinion on complex problems that require structuring. As such, the methodology can be adjusted and applied to other problems such as stock assessment and management. Indeed, Bayesian inference is increasingly used in estimating model parameters in ecology because of its ability to incorporate uncertainty and prior knowledge (Hobbs and Hilborn, 2006; Tableau et al., 2013). Our approach could facilitate the elicitation of more informative priors in a context of strong expertise on population functioning and thus improve the quality of parameter estimation and stock assessments. More readily, the EPI index scores can help to 'tune' the dispersal parameter(s) in process-based models more efficiently (GR3D; Rougier et al., 2014).

From an ecological perspective, the first application of the methodology led to ecologically meaningful results interpreted below, encouraging its future use and development. The dominant opinion among experts was that most weight should be accorded to the transfer and turn-over mechanisms when responding to directional

environmental variability. Depending on the relative importance of these two abilities for a given species, the North Atlantic anadromous species could be arranged along the known continuous gradient between the ‘capital breeding strategy’ and the ‘income-breeding strategy’ (Jager et al., 2008). The first group was described as species that store the energetic reserves and fecundity material required for infrequent breeding events, favoring somatic growth and large body size. Strict representatives of this strategy occur within sturgeons and semelparous salmonids (Jager et al., 2008). Here, body size has been unequivocally and positively correlated by experts to the transfer ability, this being in line with the common hypothesis of long-distance migratory species being larger. On the other side of the gradient, income-breeders correspond to fish with high potential for reproduction that tend to be of smaller size (Jager et al., 2008). Traits correlated with rapid life histories and population dynamics were positively related by experts to the turn-over mechanism. Examples in our list of species that most probably pertain to the second half of this continuous gradient between capital and income breeders are *Dorosoma cepedianum* and *Osmeridae* (*Osmerus mordax* and *O. eperlanus*). The three species were cited in the literature as species already exhibiting signs of climate impacts on their distribution (Limburg and Waldman, 2009; Pronier and Rochard, 1998; Waldman, 2006). These ‘quick’ reactions to climate change could be linked to their fast population growth rates, short generation times and also, most certainly, to their physiological limits. In addition, the observed distribution trends were in accordance with their relative EPI rankings, e.g. species highly ranked for movement, such as *D. cepedianum* colonizing rivers northwards. However, representatives of each strategy (i.e. capital- versus income-breeders) were dispersed along the gradient of EPI scores. This suggests that the best strategy is most probably made of a mixture of both alternative attributes. In that sense, the species that ‘outperformed’ all the others, striped bass, showed good locomotory capabilities through its large body size as well as relatively fast population dynamics (Setzler et al., 1980).

The other pattern largely shared among experts is that the exploratory potential strongly depends upon the ability to depart. Experts emphasized the role of straying for this mechanism as an ‘exploratory behavior.’ Natal homing allows species to capitalize on long-term stability, but straying is a way of enabling a rapid adaptation to a changing environment by sampling new environments. Moreover, the rate of straying is generally thought to be somehow inversely related to the stability of habitats required for ensuring offspring survival/replacement (Keefer and Caudill, 2014; Secor, 2015). However, experts when giving their opinion did not explicitly acknowledge this dynamic component of the straying process.

The last and smallest group put the accent on the departure mechanism in association with the turnover rate. In this formalization of reality, species must not only be able to sample new environments but also to do it on a highly regular basis, no matter how far individuals move at each generation.

From the present numerical application point of view, beyond the chosen paradigm, rankings were more or less identical for North-Atlantic anadromous fish. This conclusion should facilitate the transfer of EPI-based recommendations to conservationists through the identification of categories of species: those always falling in the upper or lower range versus the more undetermined ones. Here, two groups of species emerged as of particular interest: (i) three species (i.e. *Acipenser sturio*, *A. brevirostrum* and *Alosa aestivalis*) already identified as internationally threatened (IUCN criteria) with moderate to weak exploratory capacities relative to other anadromous species, and (ii) three species (i.e. *Petromyzon marinus*, *Alosa pseudoharengus* and *Coregonus* spp.) without international conservation priorities but also falling at the lower end of the ranking. For the first group, this result strongly suggests that assisted migrations (i.e. deliberately moving a plant or an animal to a different habitat) among regions or continents (Lawler and Olden, 2011) might be relevant options to consider in their restoration strategy given their low natural exploratory potential, in addition to

more common and local measures such as barrier removals to migration (e.g. dams) and stockings in existing rivers (Pess et al., 2014). For the second group, their potentially low ability to colonize new habitats outside their current continental range is also an issue that should be raised in the first place in future conservation status assessments at any level of management (i.e. federal/regional, national and more). These recommendations at the species level are in line with Hare et al. (2016)’s conclusions from a trait-based vulnerability assessment. Diadromous fishes are a group of species with a low potential for distribution change when compared with strict marine animals because of their intrinsic homing tendency. In addition, it was hypothesized that their marine distributions may be changing faster than their spawning distributions (see [www.st.nmfs.noaa.gov](http://www.st.nmfs.noaa.gov) for species ‘Fact Sheets’), potentially decoupling the suitability of spawning and growth habitats (e.g. Nye et al., 2009). These conclusions strengthened the need for diadromous fish conservation to give more consideration to shifting distribution-related issues. Recommendations could point towards the characterization of geographical areas in terms of exploratory potential of their migratory fish assemblage, or the identification of areas of special concern due to the presence of species with extremely high or low exploratory potential. Results of this work might also suggest which fish species and territories should be monitored for range expansion and the arrival of certain species respectively as effective indicators of climate change.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2018.03.047>.

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